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ANATOMY AND RELATIONSHIPS OF THE FAMILY PHLEGETHONTIIDAE (AMPHIBIA, AÏSTOPODA)

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Abstract

The cranial and cervical osteology of the middle Pennsylvanian aïstopod amphibian *Phlegethontia linearis* Cope, from Linton, Ohio, is described. *Aornerpeton mazonense* (Gregory), new genus, and *Sillerpeton permianum*, new genus and species, are compared and contrasted with *P. linearis* in endocranial structure and in the functional anatomy of their feeding mechanisms.

The feeding mechanism of *Phlegethontia linearis* is investigated. It displays cranial kinesis with unilateral jaw movements, in a manner analogous to that of snakes. The articulations of upper and lower jaws indicate a capacity to ingest large prey items, the reduction of the gastralia may have facilitated sufficient ventral distention of the body to compensate for a lack of lateral palatal mobility.

The Phlegethontiidae and Ophiderpetontidae show widely divergent cranial specializations but are related on the basis of their common and uniquely derived postcranial characters. The Aïstopoda cannot be derived from or closely related to any presently known amphibian group.

Introduction

Two genera have been included within the aïstopod amphibian family Phlegethontiidae of Cope—*Dolichosoma* Huxley, 1867, and *Phlegethontia* Cope, 1871—the former from the early Pennsylvanian of Europe, the latter from the middle Pennsylvanian to early Permian of the United States. One other family is included in the Aïstopoda, the Ophiderpetontidae. The Ophiderpetontidae contains only the genus *Ophiderpeton*, which ranges from the early Mississippian of Scotland to the middle Pennsylvanian of the United States (Baird, 1964).

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Members of the Aïstopoda are snakelike, lack either limbs or girdles, and possess holospondylous centra with intravertebral foramina and k-shaped ribs. *Ophiderpeton* has a dense dorsal and lateral covering of osteoderms on the head and body and tightly-fitting gastralia. The Phlegethontiidae lack dorsal and lateral osteoderms and have very thin, widely separated gastralia.

Dolichosoma emersoni, the type species of *Dolichosoma*, is indistinguishable from *Ophiderpeton* (Bossy, personal communication). A second nominal species, *D. longissima* Fitsch, 1875, is indistinguishable from *Phlegethontia linearis* Cope, 1871, the type species of *Phlegethontia* (McGinnis, 1967). McGinnis unfortunately used an incorrect combination, *P. longissima* (McGinnis, 1967).

P. linearis is known from the late Westphalian D of the type locality, Linton, Ohio, and from Nýřany, Czechoslovakia, the type locality of *Dolichosoma longissima*. Gregory (1948) named and superbly described a second species, *P. mazonensis*, from the early Westphalian D of Mazon Creek, Illinois. Turnbull and Turnbull (1955) added some information on skull morphology to the description of *P. mazonensis* on the basis of a second specimen. McGinnis (1967) described a phlegethontiid braincase from the early Permian of Fort Sill, Oklahoma. McGinnis (1967) synonymized all *Phlegethontia* into one species, failing to deal adequately with the limited, often crushed specimens of *P. linearis* from Linton, Ohio, and not taking into account the differences between *P. mazonensis* and the Fort Sill braincase.

Recent work at the Linton locality by Carnegie Museum of Natural History field parties has produced two additional specimens of *Phlegethontia*. One specimen, Carnegie Museum (CM) 23,053 is a well preserved skull over 27 mm in length and the other, CM 23,056, is a small individual with well preserved otic region and anterior vertebrae. Investigation of these specimens has clarified several problems in morphology, and comparison with other phlegethontiid material has resulted in new understanding of the systematics, form, and function of the members of this highly specialized family of amphibians.

The Phlegethontiidae are specialized predators with cranial kinesis and, at least in *P. linearis*, a capability for unilateral jaw motions analogous to that of snakes. Strong morphologic differences justify generic separation of *P. linearis*, *P. mazonensis*, and the Fort Sill specimen as well. These differences indicate a striking degree of functional diversification within the group and isolate them from any other known amphibia.

ACKNOWLEDGMENTS

Many thanks to Helen McGinnis for her extensive discussions and loan of photographs. Paul Harris and the Field Museum of Natural History have graciously permitted me to reproduce the photograph of FM-MCP 501. The invaluable assistance, advice, latex peels, and finally the goading of Donald Baird cannot be adequately repaid, and his expertise in naming has produced one of the new names below. Kathleen Hahn Bossy has freely discussed her work in progress. To the many persons in my field parties to Linton, and particularly to Donald Mullenaux, who found CM 23,053, my deepest gratitude.

Abbreviations.—AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, United States National Museum, Washington, D.C.; FM, Field Museum of Natural History, Chicago, Illinois.

SYSTEMATIC PALEONTOLOGY

Order Aïstopoda

Family Phlegethontiidae Cope

Phlegethontia linearis Cope, 1871

Holotype.—AMNH 6966 and counterpart 6886, from the Freeport Formation, Allegheny Group, Westphalian D, of Linton, Jefferson Co., Ohio.

Synonymy.—*Dolichosoma longissima* Fritsch, 1875.

Diagnosis.—Phlegethontiid with separate parietals, supraoccipital and tabulars composing roof of braincase; prominent sagittal crest on supraoccipital separating extensive temporal fossae posterior to pineal opening; long sphenethmoid; single, elongate, anterior foramen for cranial nerves 5 and 7; one pair of palato-braincase processes, the *tubera basisphenoidales* of Gregory (1948); rear margin of palatoquadrate vertical; ribs dorsally expanded, articulated to each other anteriorly.

Occurrence.—The Westphalian D, middle Pennsylvanian of Linton, Ohio, and Nýřany, Bohemia, Czechoslovakia.

Description

Growth.—The contention by McGinnis (1967) that the length of the snout of *Phlegethontia linearis* exhibits positive allometry relative to the skull length is not sustained either by her graph (McGinnis, 1967: Fig. 4) or by any other measurements. Within the limits of a statistically very small sample, size ratios for all measured length parameters are extremely close. Examination of specimens shows that apparent relative elongation of the snout can be accounted for by two factors—postmortem deformation of the anterior part of the premaxilla, and postmortem anterior dislocation of the premaxilla-nasal complex.

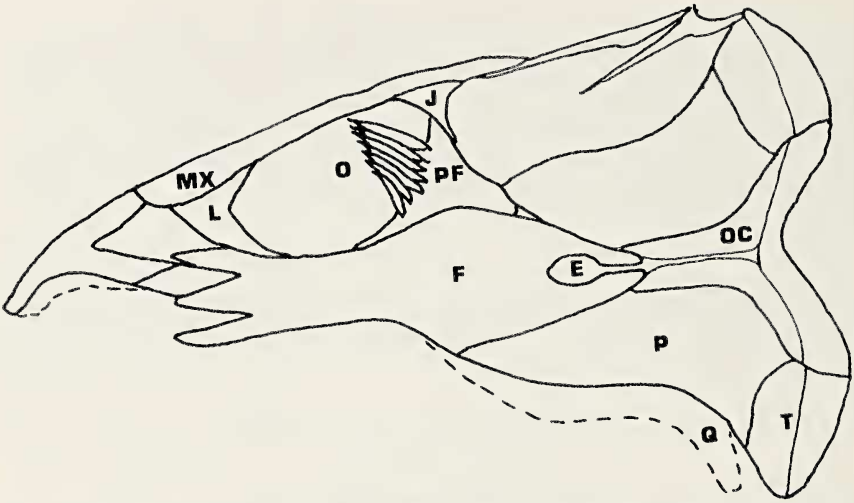

Fig. 1.—*Phlegethontia linearis*, skull roof in dorsal view. After AMNH 6966, 6886, 2564, MCZ 2038, CM 23,053. E, pineal foramen; F, frontal; J, jugal; L, lacrimal; MX, maxilla; O, orbital osteodermi; OC, occipital; P, parietal; PF, postfrontal; Q, pterygoquadrate; T, tabular.

USNM 4484, which McGinnis (1967:36) contends may be a separate species, has been subject to crushing from above and postmortem anterior dislocation and deformation. There are no reasons to believe that this specimen represents a separate species.

There is noticeable relative elongation of the circumpineal prongs of the frontal with increased size in the few specimens that display this region well. The sagittal crest is well developed on even the smallest specimen of *P. linearis*, MCZ 2038, braincase length 3.5 mm. This contrasts strongly with the lack of a sagittal crest in the type specimen of *P. mazonensis*, USNM 17,097, which is 4 mm in braincase length.

Osteology.—Examination of latex peels of all known Linton *Phlegethontia* skulls has made it possible to prepare a refined restoration of the skull (Figs. 1–2). All details have been verified in at least two specimens except for the tympanic bones. Names of the elements follow Gregory (1948) where possible.

The premaxilla has a strong ascending process, firmly joined at its dorsal margin to the nasal, and separated from its opposite in the midline by the median prong of the frontal. The facial portion of the premaxilla abuts loosely against the anterior end of the maxilla. The lacrimal abuts loosely against the edge of the lateral prong of the frontal (=fused prefrontal?) and forms the entire anterior border of the orbit. It ends ventrally in a concave face far too thick to have served merely as an

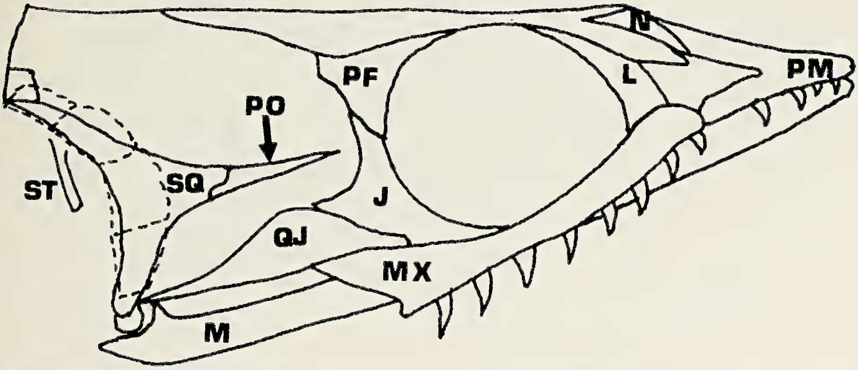

Fig. 2.—*Phlegethontia linearis*, skull restored in lateral view, tympanics dashed to show squamosal. J, jugal; L, lacrimal; M, mandible; MX, maxilla; N, nasal; PF, postfrontal; PM, premaxilla; PO, postfrontal; PM, premaxilla; PO, postorbital; QJ, quadratojugal; SQ, squamosal; ST, stapes.

articulation for the relatively thin, slightly convex anterior expansion of the maxilla. The maxilla has a slightly wavy but smooth dorsal surface, onto which fit the jugal and quadratojugal. The posterior border of the maxilla is slightly thickened, and the maxilla deepens markedly posteriorly.

The postfrontal (Figs. 2, 3) fits against the postorbital process, tapers to a point anterodorsally, and is thick at its posterodorsal end. The ventral extension is narrow, relatively thick, and bears a shallow vertical groove ventrolaterally. The dorsal half of the bone is flat in lateral aspect in AMNH 2564, and well rounded in the type specimen, AMNH 6966, but in each the ventral half is overlain by the jugal in a loose, sliding articulation that invariably hides the ventral end of the postfrontal. The jugal forms the posteroventral quarter of the orbital margin, lying against the dorsal margin of the maxilla and the anterodorsal margin of the quadratojugal. The quadratojugal is long, thinning to a feather edge dorsally except where it abuts against the jugal. It has a slightly wavy anteroventral border, which evidently fits the posterodorsal edge of the maxilla. The quadratojugal is rarely found articulated with other bones.

The squamosal complex is composed of the wedge-shaped postorbital which fits like a hinged spike onto the short anterior process of the thin, curved squamosal, and a series of four thin, flat, scale-like tympanic elements, which lie lateral to the ascending portion of the squamosal. The posterodorsal end of the squamosal contacts the posterolateral (tabular) corner of the braincase, and the ventral end contacts the quadrate region of the pterygoquadrate.

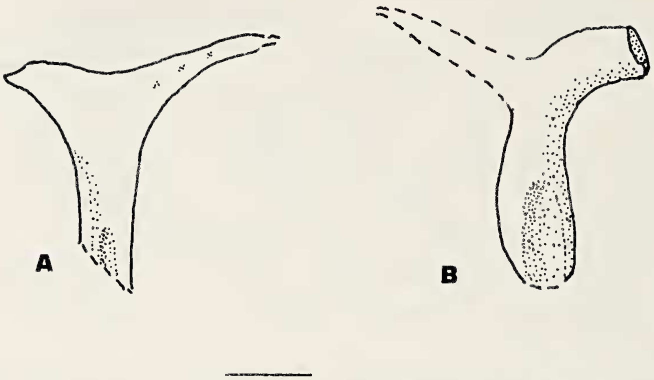

Fig. 3.—*Phlegethontia linearis*, postfrontals. A, AMNH 2564, B, AMNH 6966. Scale is 1 mm.

Several specimens, including MCZ 2038 (McGinnis, 1967: Fig. 2) have more than six thin, long, cranial osteoderms inclined anteroventrally along the posterior border of the orbit anterior to the postfrontal and jugal (Fig. 1). These elements were incorrectly identified as sclerotics in MCZ 2038 and the Mazon Creek phlegethontiid (Gregory, 1948). Sclerotics are preserved in CM 23,053.

The endocranium of *Phlegethontia linearis* consists of three closely sutured components—the frontal, the sphenethmoid, and the braincase. The frontal bears descending flanges on the ventral surface in the orbital region to which the sphenethmoid is sutured, and lies over a dorsal emargination of the braincase in the pineal region.

The sphenethmoid, a large, V-shaped ossification in transverse section, meets the braincase at approximately mid-orbit, forming the greater part of the interorbital septum and the midline of the roof of the mouth. It overlaps the anterior end of the cultriform process posteroventrally. The foramen for the optic nerve is located at the junction of sphenethmoid and braincase (Fig. 4). The olfactory nerves pass dorsally between the branches of the V to emerge at the anterior end of the element, where they are divided by a descending medial vertical septum from the preorbital portion of the frontal. This septum decreases in depth anteriorly until it vanishes at the anterior end of the central prong of the frontal.

The braincase consists of the following elements: distinct parietals dorsolaterally (Fig. 1), flooring the extensive temporal fossa; supraoccipital ridge dorsomedially, supporting the sagittal crest and not separate from the remainder of the occipital and its sharp occipital crests; small, square tabulars supporting the lateral extensions of the occipital

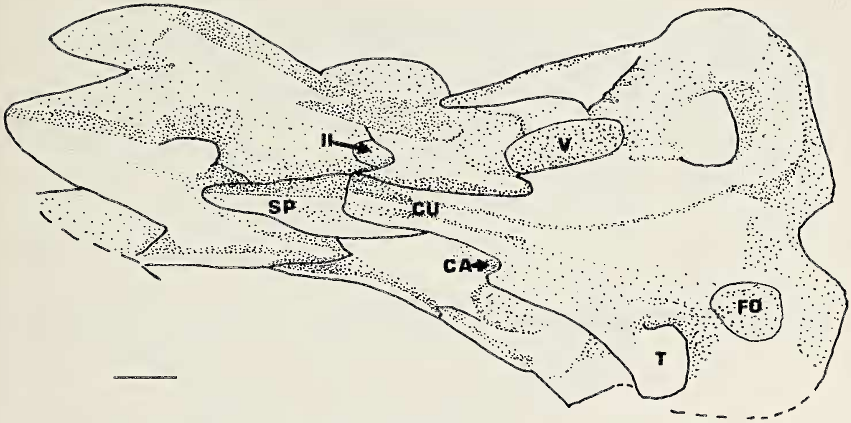

Fig. 4.—*Phlegethontia linearis*, MCZ 2334, braincase in ventral view. Scale is 1 mm. CA, carotid arterial foramen; CU, cultriform process; FO, fenestra ovalis; SP, sphenethmoid; T, *tuber basisphenoidalis*; II, optic foramen; V, foramen for nerves 5 and 7.

crests; a one piece ventral element. The braincase is structurally a single unit distinct from the frontal-sphenethmoid complex. The braincase in ventral view (Fig. 4) bears a short cultriform process, notched posteriorly for passage of the carotid arteries. Immediately posterodorsally is a single, elongate foramen for cranial nerves 5 and 7 (the "optic" foramen of Gregory, 1948). A broad anteroventrolaterally facing process, the *tuber basisphenoidalis* of Gregory (1948), projects from the ventrolateral margin of the braincase. The prominent fenestra ovalis is located near the rear margin of the braincase.

The anterodorsal margin of the braincase is deeply emarginate medially for reception of the frontal. The pineal opening is a keyhole-shaped opening in the posterior midline of the frontal. The parietals, separated in the midline, do not enclose the pineal opening anteriorly. The braincase of *P. linearis* differs from the Fort Sill braincase in features such as the position, shape, and relative size of the *tubera basisphenoidales* and carotid and prootic foramina, and in having distinct dorsal ossifications (McGinnis, 1967: Fig. 5b, c, Pl. 1C). Far more substantial differences exist between *P. linearis* and *P. mazonensis*.

The palate in phlegethontiids is composed of an anterior or palatine portion and a separate posterior unit incorporating pterygoid, epipterygoid, and quadrate. Palatal elements were loosely articulated with the remainder of the cranial elements in all known specimens, the only discrete articulatory arrangements being between epipterygoid and basicranial processes such as the *tubera basisphenoidales*. The Fort Sill

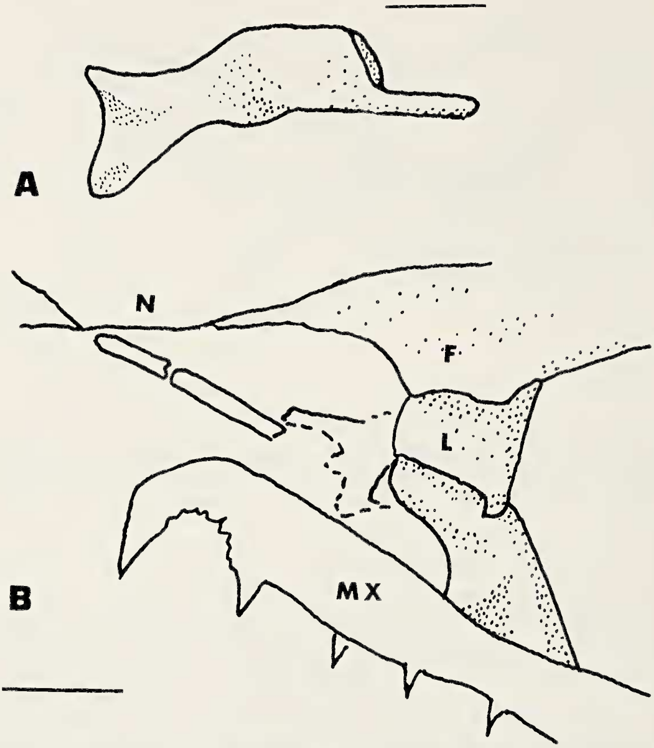

Fig. 5.—*Phlegethontia linearis*, A. MCZ 2301, ventral view of left anterior palatal element; anterior to left. Scale is 0.5 mm. B. Preorbital region of AMNH 6966. Scale is 1 mm. F, frontal; L, lacrimal; MX, maxilla; N, nasal.

braincase has a lateral facet, however, which probably articulated with the dorsal edge of the epipterygoid (McGinnis, 1967: Fig. 5).

The anterior palatal elements of *P. linearis* are known only from tantalizing fragments. An articulation between the pterygoquadrate and the anterior unit can be seen in CM 23,053. A thick, loose element in the snout of AMNH 6966 (Fig. 5B), associated with a thin anteriorly extending bar, seems to be a lateral view of an element seen in ventral view under the anterior end of the frontal of MCZ 2301 (Fig. 5A). This "palatine" is topographically associated with the anterior end of the maxilla and, through the anterior bar, with the posteroventral end of the premaxilla. No information is presently available on the anterior end of the palate of *P. mazonensis*.

The posterior, or pterygoquadrate, unit of *P. linearis* is a single element with no sutures, shaped approximately like a hatchet. It lies

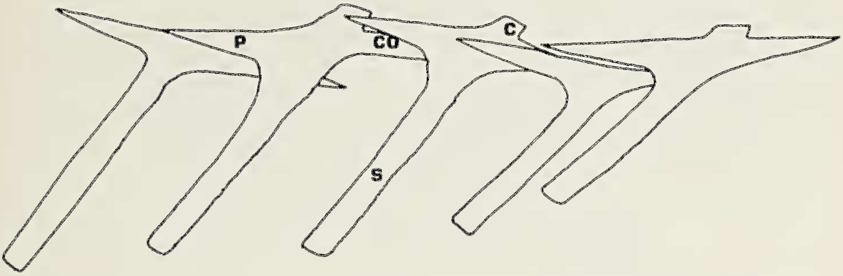

Fig. 6.—*Phlegethontia linearis*, AMNH 2564, first five ribs of right side, lateral view, C, capitulum; CO costal process; P, posteromesial process; S, shaft.

along the lateral surface of the braincase and extends anteriorly to an articulation at the level of the front of the orbit (Fig. 7). The posterior and dorsal margins are straight, and the quadrate condyle is a simple cylinder with a flared external edge. The pterygoid portion, the ''handle'' of the hatchet, is expanded only slightly at its anterior end.

Ribs.—The tetraradiate ribs of *Phlegethontia linearis* are difficult to visualize, and have been the subject of much debate (Baird, 1964). Baird's terminology for parts is used (Fig. 6). Significant differentiation of the first six ribs of the column exists, followed by gradual reduction of the specialized processes in the succeeding six ribs. The anterior ribs are each single-headed and bear a long, anteriorly directed costal process as well as a long, posteromesial process close to the capitulum. The first two ribs are short-shafted; the succeeding ribs have relatively uniform, longer shafts. The costal process of each tetraradiate rib extends ventral to the posteromesial process and mesial to the shaft of the rib anterior to it to form a tightly interlocked complex reminiscent of an avian rib cage. It seems incongruous to have the flexibility of single-headed ribs upon prominent transverse processes combined with tightly interwoven proximal regions of ribs, unless the system reflects the development of specialized cervical epaxial musculature associated with powerful support and movements of the head. Additional factors that may support this hypothesis are the following: the absence of ribs on the first two or three vertebrae; the strong transverse processes; the absence of occipital condyles; the well-defined and dorsomedially embayed occipital crest.

Aornerpeton, new genus

Type Species.—*Phlegethontia mazonensis* Gregory, 1948

Diagnosis.—Phlegethontiid with no separate dorsal ossifications in braincase; no sagittal crest; two pairs of palatobasal processes on

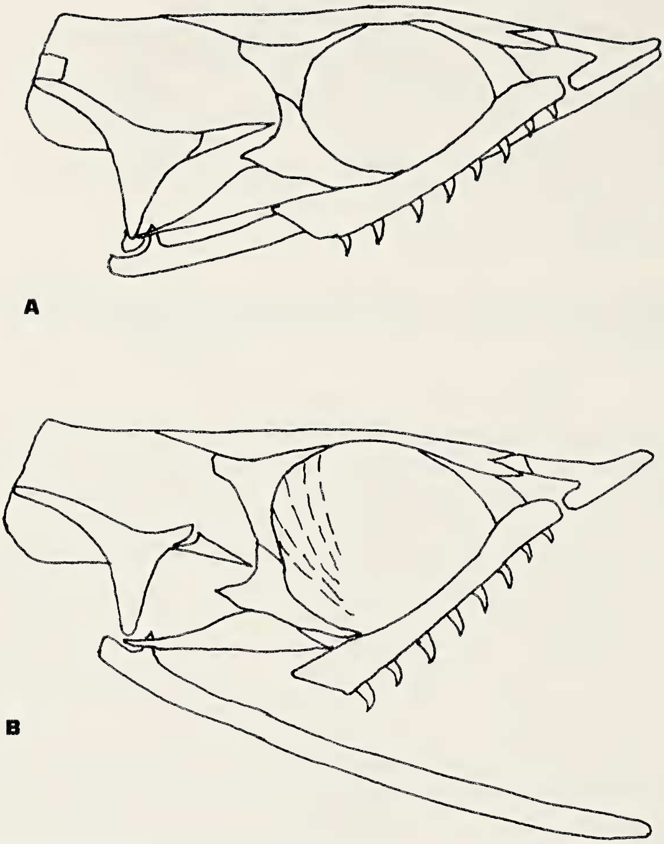

Fig. 7.—*Phlegethontia linearis*, jaw mechanics. See text for explanation.

braincase; cultriform process extending almost to anterior border of orbit; a lateral and an orbital foramen for branches of nerves 5 and 7; posterior margin of epipterygoid deeply notched dorsally lateral to lateral foramen for nerves 5 and 7; pterygoid flared anterolaterally; ribs very thin.

Derivation.—Named, as was *Phlegethontia*, for a watercourse in Hades—the river where no birds sing, according to Greek mythology.

Aornerpeton mazonense (Gregory, 1948)

Holotype.—USNM 17079.

Referred Specimens.—FM-PR 281, FM-MCP 501, MCZ 2204.

Occurrence.—Francis Creek Shale, Carbondale Formation, Pennsylvanian, early Westphalian D of Grundy and Will counties, Illinois.

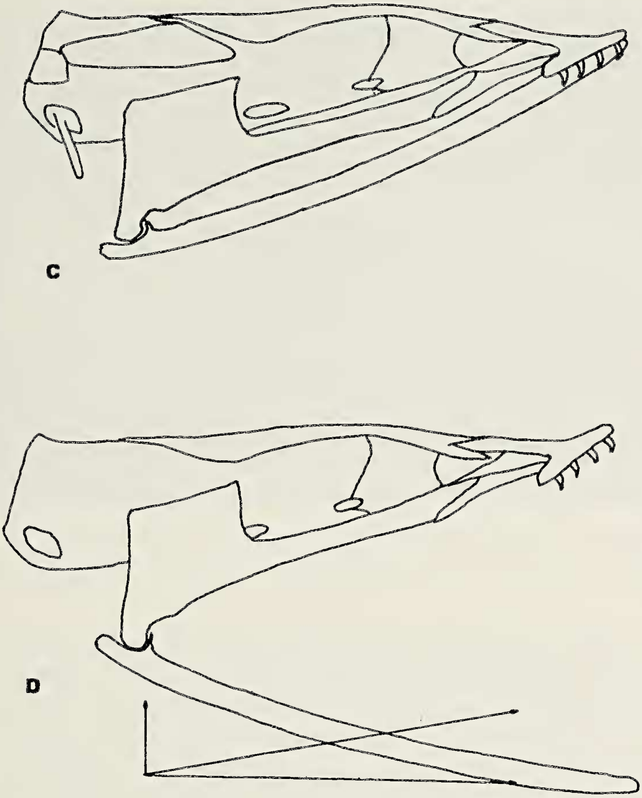

Fig. 7.—*Phlegethontia linearis*, jaw mechanics. See text for explanation.

Discussion.—Little can be added to Gregory's (1948) description of the type specimen, which has an excellent three dimensional skull lacking only the snout and several cheek bones. Characters used in the diagnosis of this genus demonstrate the great differences between *Phlegethontia* and *Aornerpeton*. Newly available material in private collections seems to bear a premaxilla of essentially similar shape and proportions to that of *Phlegethontia linearis*.

A few additional observations can be made on the known specimens of *Aornerpeton*. The lacrimal is thin laterally, but bears a mesial flange from its front edge. The elements identified as sclerotics by Gregory (1948) are relatively undisturbed orbital osteoderms. The postorbital process of USNM 17,079 is very slight and lacks a prominent groove for reception of a postfrontal in contrast to the condition in

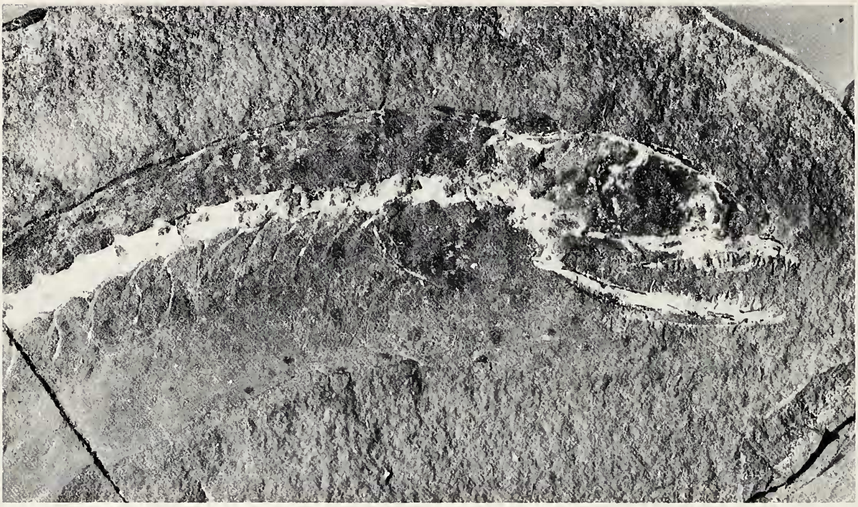

Fig. 8.—*Aornerpeton mazonense*, FM-MCP 501, Field Museum photograph. Paul Harris Collection.

Phlegethontia. A pineal opening is present in the specimen, evidently revealed by additional preparation after Gregory's description. The maxilla does not rise significantly posteriorly, unlike *Phlegethontia*, and does not extend past the rear of the orbit. The pterygoids of the type specimen (Fig. 10) are separate elements, which were originally sutured to the epipterygoids rather than fused as in the larger specimens of *Phlegethontia*. The posteroventromesial edges of the epipterygoids are somewhat upturned posterior and mesial to the *tubera basisphenoidales*. This would either effectively prevent significant palatal motion anteriorly and laterally or serve as ligamentous attachment areas for a palatobasal ligament. A prominent ligamentous scar is present on the posteroventral edge of the epipterygoid immediately in front of the quadrate process, evidently for a palatomandibular ligament that would insert anterior to the mandibular articulation. The ribs are long and very thin, although they seem to bear needle-like costal processes.

A specimen in the collection of Paul Harris (Field Museum photograph FM-MCP 501), retains a pigment pattern of three dark transverse bars at the dorsum of the neck, followed by one transverse row of dark spots on the dorsum per vertebral segment. The orbital region seems to have been all black including the top of the head, preceded by a few spots on the snout region. Smaller dark spots occur ventrally on the throat (Fig. 8, 9). The pattern of melanin markings is cryptic, disruptive

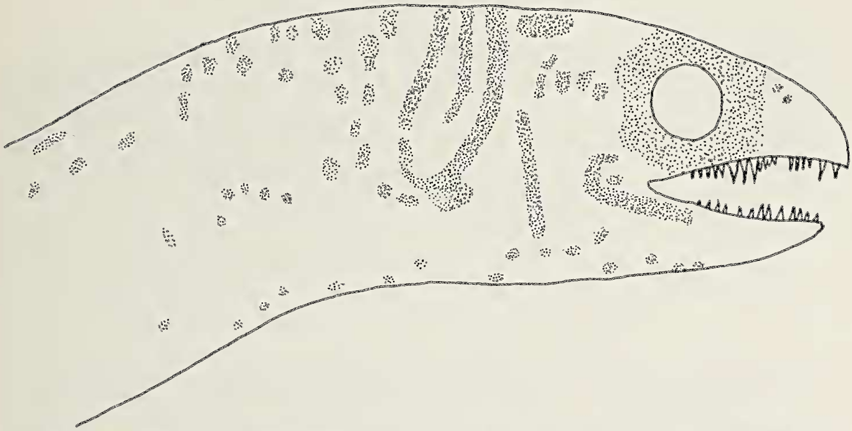

Fig. 9.—*Aornerpeton mazonense*, Color pattern and dentition. After FM-MCP 501.

coloration, comparable to that seen in juvenile *Coluber* or many other diurnal predaceous snakes (E. D. Brodie, Jr., personal communication).

Aornerpeton shows conspicuously derived character states over the condition seen in *Phlegethontia* in the degree of ossification of the braincase, the obliteration of the sagittal crest, the presence of a paroccipital process and the epipterygoid ridges associated with the *tubera basisphenoidales*, and the elongation of the cultriform process. Conditions, which seem to be plesiomorphic in *Aornerpeton*, include the presence of lateral and orbital foramina for nerves 5 and 7 (Thomson, 1965; Panchen, 1964), the notching of the margin of the epipterygoid, and the shape and independence of the pterygoid.

Sillerpeton, new genus

Type Species.—*Sillerpeton permianum*, new species.

Provisional Diagnosis.—Phlegethontiid with completely fused braincase; no sagittal crest; a fossa for articulation of the dorsal end of the epiopterygoid and narrow vertical articular *tubera basisphenoidales* for palatal articulation; cultriform process not projecting beyond edge of braincase midorbitally; single, orbital foramen for cranial nerves 5 and 7.

Derivation.—Named for Fort Sill, Oklahoma.

Sillerpeton permianum, new species

Phlegethontia cf *P. linearis* (McGinnis, 1967, fig. 5)

Holotype.—UCMP 62,480, braincase.

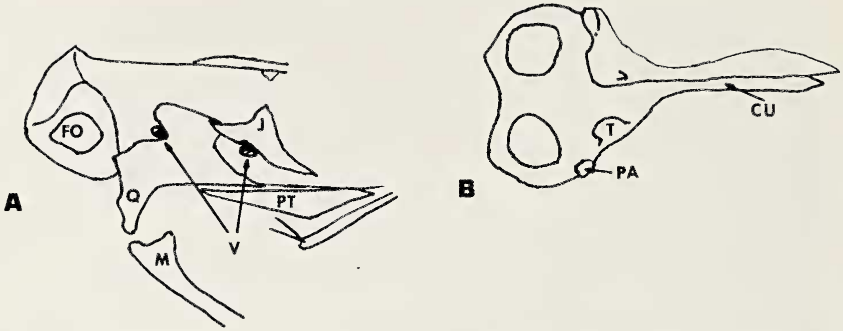

Fig. 10.—*Aornerpeton mazonense*, USNM 17,097 type. A. lateral view. B. ventral view, left side without palate; CU, cultriform process; FO, fenestra ovalis; J, jugal; M, mandible; PA, paraoccipital process; PT, pterygoid; Q, quadrate-epipterygoid; T, *tuber basisphenoidalis*; V, foramina for nerves 5 and 7.

Referred Specimens.—UCMP 62,580, braincase; UCMP 63,835, two fused vertebrae; UCMP 63,831, 63,832, 63,833, 63,834, YPM 3701, separate vertebrae. Collected by Frank E. Peabody and Wann Langston.

Diagnosis.—Same as for the genus, only known species.

Occurrence.—"Fissure deposit in the Arbuckle limestone at the Dolese Brothers Limestone Quarry, approximately 6 mi north of Fort Sill, in Sec. 31, T. 4N, R. 11W, Comanche Co., Oklahoma; University of California Museum of Paleontology Locality V5052. This locality is also known as Richard's Spur. The site has since been obliterated by quarrying operations, although bones may still be collected from other nearby fissure deposits."

"The braincase came from a block of material cemented together with calcium carbonate, collected from a vertical fissure in the Ordovician Arbuckle limestone by Frank E. Peabody in 1950. In his notes this fissure is designated as FEP 60A (for further description of the locality, see Peabody, 1961)" (McGinnis 1967).

Horizon.—Early Permian age, perhaps equivalent to the Arroyo formation, Lower Clear Fork Group of Texas (Olson, 1954).

FUNCTIONAL ANATOMY

The cranial elements of *Phlegethontia linearis* are grouped into the following functional units for subsequent discussion: snout; cheek; pterygoquadrate; palatine; endocranium; mandible.

Snout

The premaxilla, nasal, and prevomer constitute the snout. The premaxilla has a low anterior portion which curves around from the midline towards the ascending process, and bears a single line of well-spaced teeth along its ventrolateral margin. The posterior margin of the ascending process abuts against the nasal fitting into the notch between the median and lateral prongs of the frontal. Both bone junctions are narrow, smooth, rounded surfaces rather than sutures. The posterior process of the premaxilla presumably abuts against the maxilla, but there is no known line of fit in any specimen. The two premaxillae and nasals are separated from each other posteriorly in the dorsal midline by the median prong of the frontal. The prevomer is unknown. The anterior end of the premaxilla is expanded into a thin, rounded, ventrally concave cup, considerably wider than the dorsal surface of the ascending process, and not apparently sutured to the opposite premaxilla.

The two sides of the snout were loosely joined to the braincase and to each other, in a manner which would allow significant dorsoventral and anteroposterior motion and probably some degree of rotational freedom as well.

Cheek

The cheek is composed of lacrimal, maxilla, postfrontal, jugal, and quadratojugal, plus the squamosal complex.

The maxilla, bearing about six large, ankylosed teeth, is not suturally attached to any other bone, but is suspended from the frontal by the lacrimal anteriorly and the jugal and quadratojugal posteriorly.

The lacrimal forms the entire anterior rim of the orbit, fitting against the lateral edge of the frontal. The anterior edge of the lacrimal is thin, and the ventral edge is thickened as if it formed an articular facet for the dorsal edge of the anterior end of the maxilla. It is plausible that there was a structural association internally between the lacrimal, the maxilla, and the anterior palatal elements, but the nature of this association is not known. There is no visible structural element in the frontal-lacrimal junction that would prevent anterior-posterior sliding motion and lateral rotation of the lacrimal. The postfrontal is fitted against the postorbital process in a manner that would allow great lateral flexibility. The ventral portion of the lateral face of the postfrontal is flattened into a facet, which lies mesial to the dorsal process of the jugal (Fig. 3).

The dorsal process of the jugal bears a flange along its posterior edge, which projects mesially posterior to the shank of the postfrontal. Anteroventrally, the jugal is in contact with the dorsal edge of the maxilla, whereas the posteroventral edge lies upon an anterior extension of the quadratojugal. The posteroventral corner of the jugal is in contact with the anteroventral element of the squamosal complex. The quadratojugal is held between the posteroventral edge of the jugal and the posterodorsal edge of the maxilla anteriorly, and forms a straight, smooth ventral edge of the cheek posteriorly. The dorsal edge rises to a thin, rounded prominence, then descends posteriorly to produce a thin point at the posteroventral corner of the cheek.

The jugal-quadratojugal-maxilla complex apparently moved as a unit, although there were no tight sutures. The jugal was capable of a posterodorsal and anteroventral sliding motion upon the postfrontal (Fig. 7A, B).

The squamosal complex (Fig. 2) is hinged to the posterolateral corner of the braincase dorsally, to the lateral edge of the quadrate ventrally, and abuts against the posterodorsal edge of the jugal anteroventrally. The ascending process can be seen to bear an anteromesially directed edge, possibly for muscle attachment, in AMNH 6966. The sinusoidal joint between the squamosal and the postorbital would allow vertical flexion, whereas maintaining contact between the anteroventral process and the jugal, a necessity if, as assumed, the posterodorsal corner of the squamosal served as a hinge during palatal protraction (Fig. 7C, D). The tympanic bones probably anchor the tympanum, and further, were not firmly attached to the underlying squamosal, a situation suggested by CM 23,056. The tympanum would thus not be affected by normal jaw motion.

Braincase

The braincase and skull roof of *Phlegethontia* are sutured into a single unit with no readily discernible internal mobility from the anterior border of the frontal to the occiput, although a limited degree of flexibility is possible at the frontoparietal joint. The small, thick nasals fit between the prongs of the frontals, dorsal to the proximal ends of the premaxillae, in movable contact with the braincase. Preorbital and postorbital processes are equally gently rounded laterally, but lightly grooved where lacrimal and postfrontal fit. Posterior to the postorbital process there is a deeply excavated temporal fossa. The fossa is separated from its counterpart in the midline by a thin sagittal crest, and prominent occipital crests form the rear border. The floor of the fossa slopes downward and outward from the sagittal crest to about mid-height of the skull, at the level of the horizontal semicircular canal. The dorsal edge of the pterygoquadrate lies ventral and lateral to this ridge. Prominent basipterygoid processes, the *tubera basisphenoidales*, are located ventrolaterally (Fig. 4) in *P. linearis* and face anteroventrolaterally.

Pterygoquadrate

The head of the hatchet-shaped pterygoquadrate lies anterolateral to the otic expansion of the braincase (Fig. 1, 7B, C) at an angle of about 35° to the long axis of the skull. The quadrate condyle, at the posteroventral corner of the bone, is a simple hemicylinder with a posterolaterally flared end, oriented at the same angle as the dorsal edge. There is no evidence of an articular facet on the braincase of *Phlegethontia* for reception of the epipterygoid; preservation of Linton material has not favored lateral views of relatively uncrushed braincases. *Aornerpeton* has no braincase-epipterygoid articulation, whereas the braincase of *Sillerpeton* has both dorsal and lateral facets (McGinnis, 1967: Fig. 5). Palatobasal articulations of *P. linearis* and *Sillerpeton* show the possibility of anterodorsal-posteroventral sliding of the palate in relation to the braincase.

The anterior ramus of the pterygoquadrate projects forward at an angle of about 142° from the ventral third of the anterolateral edge of the posterior part. It is a strap-like, toothless bone, flaring slightly in the horizontal plane suborbitally. The anterior ramus appears to end at the anterior margin of the orbit in a ridge abutting against the palatine. In summary, the hatchet-shaped pterygoquadrate can slide anterodorsally on the basal process and abuts against the posterior end of the palatine in a movable joint.

Anterior Palatal Elements

The anterior part of the palate is best displayed in the type specimen, AMNH 6966 (Fig. 5), as a toothless strut extending from the level of the preorbital process to the region of the posteroventral end of the premaxilla. An anterior palatal element of CM 23,053 seems to bear a short lateral process or ridge which may approach the anteromesial surface of the maxilla, but additional details of the front of the palate cannot be determined.

Mandible

Two elements comprise the mandible, the dentary laterally and the postdentary mesially. The postdentary lies internal to the dentary from the symphysis back, almost totally overlapping it. There do not appear to be any sutures uniting the two elements, and as the elements are usually rotated with respect to each other in the fossils, the connection must have been predominantly ligamentous in nature. Symphyseal contact between mandibles was by small flat surfaces and there was no fusion in the midline. The articular fossa, oriented perpendicular to the long axis of the mandible, consists of a forward face, slightly convex posterodorsally, and a ventral face which is slightly convex upward.

This unusual shape is said to be more prominent in larger individuals (McGinnis, 1967). The quadrate-mandibular joint is quite smooth, and was evidently not finished in cartilage. Articulation between quadrate and mandible must therefore have been loose, the mandible capable of considerable rotation about its long axis with respect to the quadrate, as well as lateral rotation. The articular process of *P. linearis* is somewhat longer than the length of the quadrate condyle, presumably serving for insertion of a *depressor mandibularis* muscle. There are also separate, S-shaped ''hyoid'' bones posterior to the skull of *Phlegethontia*, a possible indicator of strong hypoglossal musculature.

Cranial Kinesis

Although details of the palatal osteology of *Phlegethontia linearis* remain obscure, enough information is now available to permit a reasonably accurate assessment of its cranial mechanics. Four principal functional units of the skull—snout, braincase, pterygoquadrate, and palatine—form a four-bar kinematic chain. The solidly ossified braincase is the fixed bar, as is typical for other kinetic skulls (Gans, 1961). The pterygoquadrate and palatine are struts for transfer of motion, and the snout, which bears lateral teeth, serves as the focus of the effort. The cheek with four functional units—the lacrimal, maxilla, postfrontal, and the orbital segment of the braincase—forms a dependent four-bar chain suspended lateral to, but sharing a portion of, the fixed bar of the principal chain. The dependent chain is tied, apparently closely, to the principal chain at the maxillo-premaxilla contact, possibly to the palatine, and probably by connective tissue associated with part of the *adductor mandibularis* complex to the pterygoquadrate. An ectopterygoid, if present, must have been attached loosely to the maxilla and pterygoquadrate. The posterior end of the maxilla was probably also ligamentously tied to the mandible. Motion of the maxilla, the other tooth-bearing bone of the upper jaw, while derived from motion of the principal chain, would be different from motion of the principal chain as a result of the suspension of the cheek. Protraction of the pterygoquadrate would result in anterolateral motion delivered to the palatines, and consequently an upward rotation of the snout about the dorsal hinge (Fig. 7). Retraction of the pterygoquadrate would depress the snout. Based upon scale models, a rotation of 8° of the pterygoquadrate could result in a rotation of the snout on the order of 30°.

Protraction of the pterygoquadrate (Fig. 7A, B) would result in an anterior rotation of the maxilla about its articulation with the lacrimal, ventral sliding of the jugal on the postfrontal joint, and potential laterodorsal rotation of the cheek on its braincase hinges. The cheek is reinforced by the postorbital osteoderms and the squamosal-postorbital-quadratojugal complex. The osteoderms are oriented along lines from the postorbital process to the orbital edge of the maxilla as would be heterotopic ossifications in tendons. Rotation of the squamosal complex would occur with opening of the mouth, as in Fig. 7. Retraction of the pterygoquadrate would draw the maxilla and cheek posteromesially and dorsally.

Several features stiffen or otherwise limit free motion. The nasals, braced but not sutured in the notches at the anterior end of the frontal, provide a flexible limit to dorsal displacement of the premaxillae. The suspension of the cheek from the posterodorsolateral edges of the preorbital processes indicates a limited anterior rotation around these points and a large lateral component to the motion. The condition of the cheek-braincase suspension is similar to that described in the upper Cretaceous *Dinilysia* (Frazetta, 1970). In both animals elastic connective tissue at the nasal hinge and the cheek-braincase pivots would allow some motion, yet aid in return of the joints to a resting state.

Unilateral Jaw Motion

The long, slender mandible has several remarkable features. The shape and orientation of the glenoid fossa with respect to the quadrate condyle indicates an exceedingly flexible articulation. The quadratomandibular joint is capable of sustaining considerable rotation around the long axis of the mandible, and, equally importantly, lateral deflection of the mandible about the joint in excess of 60°. A large vertical swing is also probable. The apparent relatively loose connection of the dentary and postdentary might also allow some rotation of the tooth-bearing portion of the jaw about the long axis, possibly to relieve stress in the long, thin element. The mandibles were neither fused nor sutured at the symphysis and were probably bound elastically.

All details of the lower jaws indicate that they were articulated to allow great freedom of unilateral motion. The snout is also composed of clearly independent premaxillae with no tight contact in the midline, and capable of rotation about their long axes as well as lateral displacement. The cheek suspension and the nature of pterygoquadrate articulation also indicate anterolateral-posteromesial motion of the upper jaws. Frazetta (1970) has emphasized the importance of longitudinal rotation and lateral displacement of the snout elements to an effective system of unilateral feeding motions. It seems virtually certain that the feeding mechanism of *Phlegethontia* was capable of, and adapted for, unilateral motion of mandibles and upper jaws, and not for an inertial feeding system with simple cranial kinesis for increased mechanical advantage. The unilateral system is best known in snakes, as an adaptation for swallowing oversized prey (Gans, 1961), and is unknown in modern amphibians.

Several additional observations reinforce the unilateral feeding hypothesis. The teeth, which increase in size from the front of the premaxilla back to the end of the maxilla, are recurved and slightly compressed, for piercing and holding, and like those of the snakes are best disengaged by a forward sliding motion (Gans, 1961). The well ossified braincase coupled with the shift of the kinetic joint in the skull from the frontoparietal suture typical of crossopterygians (Thomson, 1967; Panchen, 1964) to the premaxilla-braincase zone (Frazetta, 1962, 1966, 1970) and the addition of a dependent chain, indicates an increase in complexity of kinesis with a decreased emphasis on the vertical force of the bite delivered by the jaws. The snout is essentially unbraced vertically, the maxilla is hung from the braincase without vertical bracing and the mandibles show great freedom of motion about the quadrate. None of the biting units are built for sustaining vertical stresses, all are built for sustaining longitudinal and transverse motion.

Development of a large temporal fossa indicates a strongly differentiated set of mandibular adductor muscles, probably at a complex level of neuromuscular control, and probably also associated with strong hypoglossal muscular action. The flexibility of the quadratomandibular articulation, cheek, and muzzle, and the mobility of the palate indicate a distensible gape of the mouth. The posteroventral movement of the palate during unilateral jaw closing would force prey objects ventrally and into the oesophagus, aided by the ratchet action of the teeth. In this connection it is tempting to speculate that the reduction in gastralia from a condition like that in *Ophiderpeton* to thin, widely spaced bones barely discernable in the fossils would facilitate ventral distention of the body during swallowing of large prey items. The snakes, with streptostylic quadrates and limited quadratomandibular freedom, have lateral distention of the gape as well and, with the freeing of the supratemporal at the crotaloid level, distention far in excess of that possible in *Phlegethontia*.

Muscular Anatomy

Comparison with the cranial anatomy of *Paleoherpeton* (Panchen, 1964) suggests a tentative reconstruction of the jaw musculature of *Phlegethontia*. Differentiation of the *adductor mandibularis* into three muscles, *m. pterygoideus*, *m. adductor mandibularis internus*, and *m. adductor mandibularis externus*, is entirely plausible. Posteromesial to the quadrate of *Sillerpeton* is a prominent muscle scar (McGinnis, 1967: Fig. 5) which may have served as the origin of *M. adductor arcus palatini*. *M. levator arcus palatini* probably originated on the posterior edge of the postorbital process and adjacent temporal fossa. The separate S-shaped "hyoids" probably were the origin of the hypoglossal muscle.

The *adductor mandibularis externus* of *Phlegethontia* would originate from the temporal fossa, particularly from the sagittal and occipital crests, and insert on the dorsal and lateral surfaces of the postdentary *M. add. mand. internus* would originate on the lateral face of the pterygoquadrate and insert on the coronoid process and posteromesial surface of the postdentary. *M. pterygoideus* would originate on the pterygoid and insert on the mesial surface of the postdentary, *M. levator arcus palatini* and *adductor arcus palatini* would both insert on the anteromesial surface of the postdentary, and therefore far from the articulation or fulcrum of the mandible. The mechanical effects of a *depressor mandibularis* muscle, if present, would be negligible by contrast to that of the hypoglossal musculature.

Opening of the mouth by means of the hypoglossal muscles could be resolved into forces about the jaw joint as illustrated in Fig. 7D. These forces would tend not to move the pterygoquadrate until mandibular opening exceeded a critical angle of about 30°. Once this angle is exceeded, any further force tending to widen the angle of the gape would result in an anterior component of force applied to the pterygoquadrate, which would result in elevation of the premaxilla and a forward shift of the cheek. Closing the mouth would reverse the process, aided by the adductor musculature, including *m. pterygoideus*.

The double faceted glenoid fossa of the mandible plays a critical role in mouth opening and cranial kinesis. The normal or ventral surface of the fossa would be the principal pressure bearing surface during initial opening of the jaws or ingestion of small prey items. As jaw opening passed the 30° angle, the vertical component of force at the jaw joint would be borne by the anterior face, and the horizontal component of force would be transferred through the ventral face, bringing the kinetic mechanism fully into play.

Feeding Mechanism of Aornerpeton

The feeding mechanism of *Aornerpeton* is distinctive from that of *Phlegethontia*, as indicated by the bracing of the palate, proportional differences in the areas of origin of palatal musculature and the shape of the lacrimal. The snout is flexibly attached to the braincase, and the maxilla is capable of rotation around the lacrimal joint aided by ventral sliding of the postfrontal-jugal joint. Palatal sliding is seemingly limited by the two palatobasal articulations, anteroposterior motion of the lacrimal is precluded by its mesial lamina, and unilateral jaw action is virtually ruled out by the profile of the dentition. Understanding of relationships between the snout and the maxilla and palate awaits the

Table 1.—*Comparison of the braincases of three genera of phlegethontiids.*

Phlegethontia	*Aornerpeton*	*Sillerpeton*
Braincase of several bones	solid unit braincase	solid unit braincase
short cultriform process	long cultriform process	no projecting cultriform
single prootic foramen	prootic and lateral foramina	single prootic foramen
broad ventral *tubera basisph.*	broad ventral *tubera*	narrow vertical *tubera*
no "paroccipital" process	a "paroccipital" process	incipient paroccipital process
no dorsal epipterygoid articulation	no dorsal epipt. artic.	dorsal epipterygoid articulation
sagittal crest	no sagittal crest	no sagittal crest
small fenestra ovalis	large fenestra ovalis	large fenestra ovalis
narrow pterygoid	flared pterygoid	

preparation of additional specimens of *Aornerpeton*. *Aornerpeton* probably was a kinetic inertial feeder with mobile maxillae and a flexibly attached snout.

It is conceivable that *Aornerpeton* rooted in soft mud or leaf litter for food, approaching a burrowing habit. There are, however, no sutural specializations or structural braces, as seen in the skulls of amphisbaenids (Zangerl, 1944) for a strictly burrowing mode of life.

DISCUSSION

Generic Relationships

Phlegethontia linearis occurs in the late Westphalian D of Ohio (and Bohemia), *Aornerpeton mazonense* in the early Westphalian D of Illinois, and *Sillerpeton* in the Autunian (Wolfcampian) of Oklahoma. Morphologic relationships between the three are not related to time of occurrence, and signify a longstanding and broad-scale adaptive diversification. Comparison of the braincases of the three reveals the depth of this diversity (Table 1).

Aornerpeton, the oldest, and *Sillerpeton*, the youngest, share the advanced fusion of braincase, the lack of a sagittal crest, and the large fenestra ovalis, all presumably derived from a *Phlegethontia*-like condition, although size of the fenestra ovalis may be inversely related either to the size or to the age of the animal. Additionally, the structure McGinnis (1967: Fig. 5a, c) calls a "muscle scar" in *Sillerpeton* may be an incipient "paroccipital" process, as in *Aornerpeton*. There is little difference between *Phlegethontia* and *Sillerpeton* in size of cultriform process, which may be plesiomorphic, and in the prootic foramen, which may be derived (Panchen, 1964). *Phlegethontia* and *Aor-*

nerpeton have similar *tubera basisphenoidales*, and similarly lack a dorsal shelf for epipterygoid articulation.

Clearly, although the three are related, they are divergent. The palate of *Sillerpeton* may have been capable of considerable rotation about the dorsal articulation, which, guided by the *tubera*, would have translated into anteroposterior swing. This must remain speculative until more of this animal is found, but palatal articulation, and therefore the nature of the feeding mechanism, is not derivable from either the *Aornerpeton* or *Phlegethontia* conditions. Thus, although only the braincase of *Sillerpeton* is known at present, it is sufficiently distinctive to warrant generic separation.

Habitat

Many anatomical features of the Phlegethontiidae argue for primarily terrestrial adaptations. The large tympanum and narrow-shafted stapes are indicators of terrestrial sound reception. There are no traces of branchial or hyoid elements which might have supported an oropharyngeal pump or gills. The "hyoids" are not connected in the ventral midline, lie posterior to the skull, and could have acted only as origin and insertion for hypoglossal and trunk musculature. There is no indication of a larval, or less ossified stage of development. The vertebrae, with stout transverse processes, have very low spines, unlike vertebrae in amphibians which swim by lateral undulation, such as the urocordylid nectrideans (Baird, 1965). Phlegethontiids, like many snakes, may have entered the water to feed, but were primarily terrestrially adapted.

Relationships with other Families

The Ophiderpetontidae share a number of unique derived postcranial characters with phlegethontiids. These are the large number of trunk vertebrae, over 100 (Baird, 1964), and the form of these vertebrae, the total lack of limbs and girdles, and the K-shaped ribs. *Ophiderpeton* shows extreme postorbital elongation, a very short snout, no skull roof fusions, retention of simple, primitive premaxillae, and posttemporal emargination of the skull. The palate and cheek are primitively laterally mobile, articulating with the ventral edge of the skull roof. The palate projects posteroventrally beyond the skull, and articulates with a plesiomorphous lower jaw. Cranial osteoderms cover the outside of the skull, a peculiarly apomorphic character. Characters in ophiderpetontid skull evolution are opposite in direction to those of the phlegethontiids, indicating sister groups with a basic lateral undulatory propulsive system but diverging on feeding adaptation.

Among known early Mississippian Amphibia, the postorbital elongation of the skull and large number of trunk vertebrae of the adelogyrinid microsaurs (Carroll and Baird, 1968) are reminiscent of trends toward aïstopods. Loss of cheek and palatal mobility, and retention of weak limbs and girdles (Thomson and Bossy, 1970) indicate a sister group status at best.

The urocordylid Nectridea, currently under investigation by Bossy, are represented by several individuals with skulls in the Carnegie Museum collections from Linton, Ohio. These specimens, which are close to *Ptyonius*, show lateral cheek and palatal mobility, a postfrontal-jugal joint, and a supratemporal which lay loosely over a secondary sutural connection between parietal and tabular. The fossa formed in this manner is analogous to the temporal fossa of *Phlegethontia*. Cranial kinesis is present in *Ptyonius* centering around a frontoparietal joint and seeming to involve the entire snout, cheek, and palate rotating about the otico-occipital portion of the skull (Thomson and Bossy, 1970).

As Thomson and Bossy (1970) have indicated, particular sets of skull bone arrangements have specific functional determinants. Similarities between *Ptyonius* and *Phlegethontia* in skull bone arrangement involve patterns adapted from common ancestors with cranial kinesis, perhaps ancestors little modified from the crossopterygian kinetic mechanism, and these patterns have evolved along pathways dictated by functional necessities such as the development of a temporal fossa for expanded palatal musculature. Similarities between these two genera are put into perspective by the differences between *Sauropleura*, *Urocordylus* (Thomson and Bossy, 1970), and *Ptyonius* among the urocordylids, (Baird, 1965). The urocordylid Nectridea differ still further from the derived keraterpetontid Nectridea, a group with totally akinetic skulls, lacking a separate supratemporal element. All Nectridea do share a basically similar cranial osteology, similar vertebrae, elongation and compression of the tail, and a secondarily permanent aquatic habitat. Characters shared between Nectridea and Aïstopoda seem either to be plesiomorphous, or to be shared on the broadest subdivision of the Paleozoic Amphibia.

The Anthracosauria retain lateral cheek and palatal mobility and potential for cranial kinesis (Thomson and Bossy, 1970). Further, differentiation of neck and trunk vertebrae and the pattern of centrum formation are close to that of *Phlegethontia*. The anthracosaurs seem to retain features of a feeding mechanism in common with the aïistopods and with more generalized nectrideans.

Comparison with Snakes

The functional morphology of snake skulls has been analyzed in detail by Frazetta (1962, 1966, 1970) and Gans (1961, 1973). The jaws of snakes differ in many respects from those of *Phlegethontia*, but particularly in the reduction of the premaxillae, teeth on the palatines, the loose suspension of the quadrate from the rear of the skull, the tight quadratomandibular articulation, and the dentary-surangular joint. The snakes can be roughly divided into three major levels of organization, boid, colubroid and crotaloid (Frazetta, 1970; Gans, 1961), on the basis of increased freedom of motion of the maxilla and supratemporal. *Phlegethontia* can be compared to the boid level of organization, somewhat advanced over the relatively stiff suspension of the cheek and snout in the upper Cretaceous snake *Dinilysia* (Frazetta, 1970). The active role played by the *pterygoideus*, *protractor* and *retractor pterygoidei* in the movement of both maxilla and palates of snakes (Frazetta, 1966) suggests a similar function of these muscles in *Phlegethontia*. The role of mandibular and palatal rotation in the swallowing of very large prey (Frazetta, 1970) is also analogous to the articular arrangements of *Phlegethontia* between premaxilla, cheek, and braincase, in the apparently loose articulation between the rear of the maxilla and the pterygoquadrate, and in the quadratomandibular articulation. *Phlegethontia*, although phyletically unrelated to snakes, parallels them closely in body form and cranial function.

SUMMARY

The cranial and cervical osteology of *Phlegethontia linearis* is described, and that of *Aornerpeton mazonense* (Gregory, 1948) and *Sillerpeton permianum*, new genera, are compared and contrasted with it. The three genera differ greatly in endocranial structure and in the functional anatomy of their feeding mechanisms.

The feeding mechanism of *Phlegethontia linearis* displays cranial kinesis with unilateral movement of the jaws, in a manner analogous to snakes. Four principal functional units of the skull, the snout, braincase, pterygoquadrate, and palatine, form a four-bar kinematic chain. The cheek, composed of lacrimal, maxilla, postfrontal, and jugal, is suspended from preorbital and postorbital processes of the braincase as a dependent four-bar chain and is linked to the rear of the braincase and palate by the squamosal, postorbital, and quadratojugal. The mandible serves as the lever initiating kinesis when depression exceeds a critical angle. Teeth, borne on the rim of the mouth only, are strong and recurved, and aid in unilateral feeding motions. The articular arrangements of the upper and lower jaws indicate a capacity to ingest large prey items, and although the pterygoquadrates are incapable of significant lateral dislocation, structure of the jaw joint and reduction of the gastralia may indicate that the ventral surface of the body was capable of considerable distention.

The feeding mechanism of *Aornerpeton* lacks the palatal mobility of *Phlegethontia*, possibly indicating an inertial feeding mechanism. The

upper jaw and cheek bones, however, are capable of motion analogous to those of protacanthopterygian teleosts.

Postcranial characters unite the functionally diverse Phlegethontiidae with the very differently specialized Ophiderpetontidae. Of the other lepospondylous amphibians the urocordylid Nectridea share primitive characters of the feeding mechanism, but exhibit certain postcranial trends unlike those which could have led to the aïstopod propulsive system. The adelogyrinids show such trends, however, and might be a sister group. The Anthracosauria share characters of the feeding mechanism derived from the same basal condition as both Nectridea and Aïstopoda, and seem to share vertebral centrum formation and differentiation of a neck in common with phlegethontiids. There is little direct evidence for deriving the aïstopoda from any presently known amphibian group.

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